

Linking landscape-scale differences in forage to ungulate nutritional ecology

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Abstract. Understanding how habitat and nutritional condition affect ungulate populations is necessary for informing management, particularly in areas experiencing carnivore recovery and declining ungulate population trends. Variations in forage species availability, plant phenological stage, and the abundance of forage make it challenging to understand landscape-level effects of nutrition on ungulates. We developed an integrated spatial modeling approach to estimate landscape-level elk (*Cervus elaphus*) nutritional resources in two adjacent study areas that differed in coarse measures of habitat quality and related the consequences of differences in nutritional resources to elk body condition and pregnancy rates. We found no support for differences in dry matter digestibility between plant samples or in phenological stage based on ground sampling plots in the two study areas. Our index of nutritional resources, measured as digestible forage biomass, varied among land cover types and between study areas. We found that altered plant composition following fires was the biggest driver of differences in nutritional resources, suggesting that maintaining a mosaic of fire history and distribution will likely benefit ungulate populations. Study area, lactation status, and year affected fall body fat of adult female elk. Elk in the study area exposed to lower summer range nutritional resources had lower nutritional condition entering winter. These differences in nutritional condition resulted in differences in pregnancy rate, with average pregnancy rates of 89% for elk exposed to higher nutritional resources and 72% for elk exposed to lower nutritional resources. Summer range nutritional resources have the potential to limit elk pregnancy rate and calf production, and these nutritional limitations may predispose elk to be more sensitive to the effects of harvest or predation. Wildlife managers should identify ungulate populations that are nutritionally limited and recognize that these populations may be more impacted by recovering carnivores or harvest than populations inhabiting more productive summer habitats.

Key words: body condition; bottom-up; *Cervus elaphus*; elk; forage quality; summer range.

INTRODUCTION

The recovery of large carnivores such as wolves (*Canis lupus*), mountain lions (*Felis concolor*), and grizzly bears (*Ursus arctos*) across western North America has led wildlife managers to focus on understanding effects of top-down predation forces on large herbivore populations. These top-down effects are important because predation may be a proximate limiting or regulating factor for many ungulate populations (Hebblewhite et al. 2002, Garrott et al. 2008, Andren and Liberg 2015). However, establishing causation of top-down predation in driving ungulate population dynamics is difficult because predation may be partially compensatory with bottom-up nutritional or climate-mediated effects (Linnell et al. 1995, Shallow et al. 2015). Broad-scale syntheses show that predation influences prey

populations most significantly in ecosystems with low productivity or harsh winter severity (Crete 1999, Melis et al. 2009, Andren and Liberg 2015). Therefore, understanding how bottom-up forage effects on nutritional condition mediate the strength of top-down predation is important to understanding the effects of recovering carnivores on ungulate population dynamics. However, evaluating bottom-up forage effects on nutrition and reproductive performance is challenging.

Ungulate population dynamics are commonly driven by a combination of adult female survival and juvenile recruitment (Gaillard et al. 2000). In particular, nutritional condition influences maternal body condition, pregnancy rates, body size, survival, and vulnerability to predation in ungulates (Parker et al. 2009). Additionally, through the effects on maternal body condition, nutritional condition may affect fetal in utero survival, neonatal birth mass, neonatal survival, and juvenile overwinter survival (Tveraa et al. 2003, Bishop et al. 2009, Griffin et al. 2011, Shallow et al. 2015). Nutritional effects

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during juvenile development may also induce cohort effects that influence long-term reproduction and vulnerability to predation (Solberg et al. 2007, McLoughlin et al. 2008). Thus, ungulate population dynamics are expected to be affected by bottom-up factors, but assessing relationships can be challenging (Cook et al. 2013).

In practice, it is difficult to understand the relative strengths of top-down and bottom-up effects on ungulate population dynamics (Hebblewhite 2007). With widespread, long-term declines in ungulate recruitment and the successful restoration of large carnivores across western North America (P. Lukacs, *unpublished manuscript*), a critical issue for many wildlife managers is whether to improve nutritional resources by enhancing habitat or to reduce predation by managing large carnivores when trying to increase ungulate populations. The focus of public opinion often centers on management of carnivores. However, the efficacy of using carnivore reduction as the exclusive management tool to increase ungulate populations is questionable, and results may be short-lived (National Research Council 1997). Additionally, the effectiveness of carnivore management in low productivity habitats may be limited if bottom-up nutritional effects are driving population dynamics. Thus, understanding how habitat and nutritional condition affect ungulate populations remains a priority for guiding management actions.

Land management may affect ungulate nutritional resources by manipulating vegetation with grazing (Vavra and Sheehy 1996, Stewart et al. 2002, Vavra et al. 2007), fire (Long et al. 2008), or timber management (Irwin and Peek 1983, Visscher and Merrill 2009). Decades of fire suppression on public lands may have landscape-scale effects on elk (*Cervus elaphus*) habitat and the nutritional resources available to ungulates. Fire suppression may reduce the quality and extent of ungulate habitat by allowing succession to plant communities with lower capacity to support ungulates. Elk habitat on public land is typically managed for habitat effectiveness on summer ranges, providing security cover on fall ranges to minimize harvest mortality and providing adequate forage and protection on winter range. These land management strategies are based on the assumption that nutritional limitations for elk are primarily on winter range. However, much recent work suggests that ungulate nutritional requirements during summer influence ungulate reproduction and survival (Cook et al. 2013, Monteith et al. 2013). These findings highlight the need to improve our understanding of nutritional resources available during the summer growing season.

During summer, female ungulates require sufficient biomass of high quality forage to compensate for poor forage quantity and quality during winter, recover the costs of lactation, and build body reserves to survive and maintain pregnancy during the winter (Cook et al. 2004). In addition to the abundance of forage biomass, forage

quality (i.e., the energy or nutrient concentration in forage) also plays a role in the ungulate nutritional landscape. Unlike forage abundance, forage quality declines as the growing season progresses due to the accumulation of plant lignins, hemicellulose, and cellulose in plant support tissues (Van Soest 1982, Parker et al. 2009). Thus, the highest quality forage for ungulates is usually available when plants first emerge in spring, and this phenological green-wave is the driving mechanism for ungulate resource selection and migration (Fryxell et al. 1988, Sawyer and Kauffman 2011, Bischof et al. 2012). Recent studies show that the quality of forage consumed during late summer and early fall is critical for predicting vital rate responses of adult female ungulates to habitat (Cook et al. 2004, 2013). This dichotomy between quantity and quality requires estimates of both forage indices during late summer to evaluate availability of nutritional resources and the consequences of nutrition to ungulates.

A challenge to understanding landscape-level effects of habitat on ungulate nutrition is the variability in species composition, phenology, and abundance of forage species across a landscape. Early studies used reductionist plot-based approaches (e.g., Daubenmaier frames) to estimate forage. Recent studies have used a combination of plot-based methods, remote sensing-based vegetation indices, such as the normalized difference vegetation index (Pettorelli 2013), and spatial modeling to predict forage across larger landscapes (Hebblewhite et al. 2008, van Beest et al. 2010, Pretorius et al. 2011). The benefit of this approach is that forage availability, phenological stage, and digestibility can be integrated to produce landscape-scale predictions of nutritional resources that can then be related to ungulate exposure to nutritional resources and vital rates.

Our goal was to use an integrated spatial modeling approach to evaluate elk nutritional resources in two adjacent study areas that differed in coarse measures of habitat quality and relate the consequences of potential differences in nutritional resources to elk body condition and pregnancy rates (Fig. 1). The study area has recently experienced large-scale wildfires, as well as wolf restoration and increasing mountain lion populations, highlighting the need for evaluating both bottom-up and top-down effects on the elk populations. We developed a landscape-scale nutritional resources model and then compared nutritional resources on elk seasonal ranges in the two study areas to the body condition and pregnancy rate of adult female elk in each area. We predicted that elk on summer range with lower nutritional resources would have lower body condition and pregnancy rates (Cook et al. 2013, Monteith et al. 2013). We tested the hypothesis that phenological stage differences in forage between the study areas may drive differences in nutritional resources. Finally, although recent work has focused on the relationship between summer nutrition and ungulate body condition and vital rates, we also tested for differences in winter nutritional resources

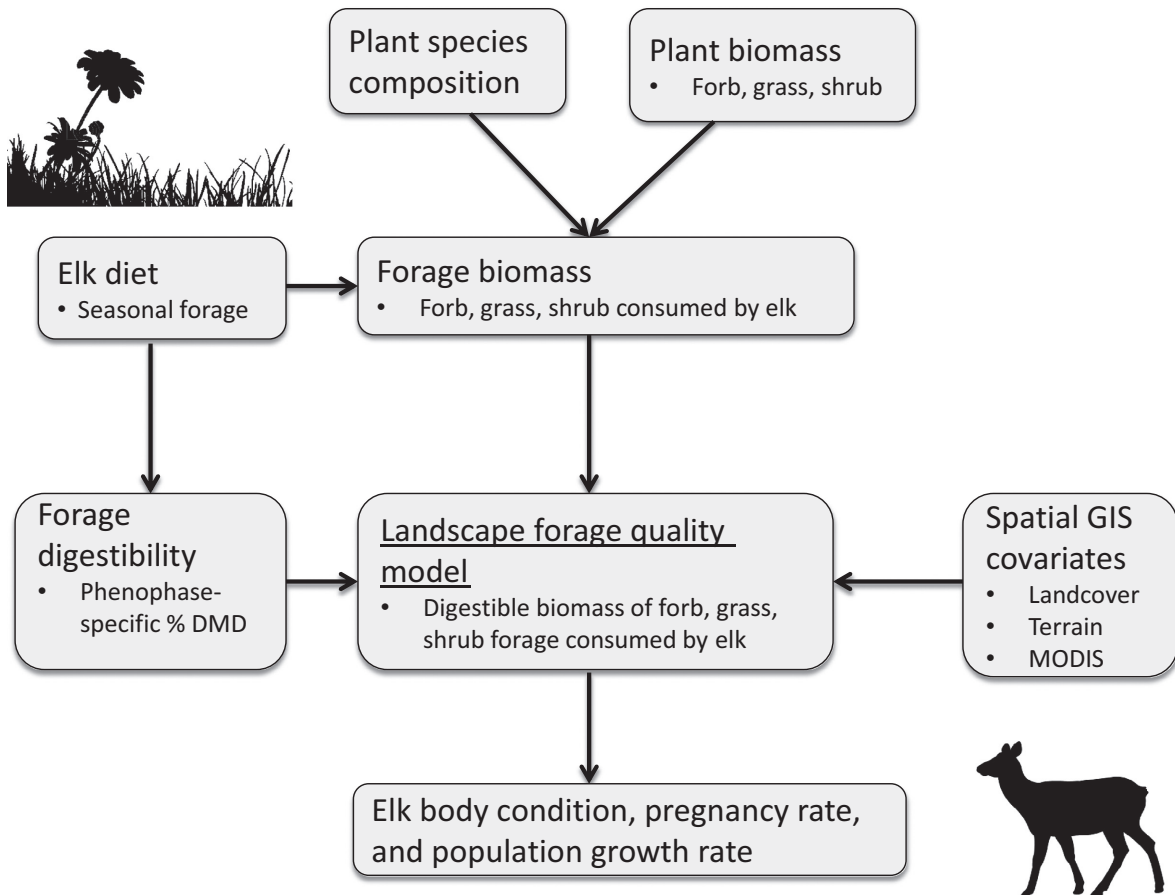


FIG. 1. Conceptual figure of the landscape nutritional resources model developed for elk (*Cervus elaphus*) in the southern Bitterroot Valley of western Montana, USA, 2012–2013. Plant species composition and biomass was estimated at 236 sampling sites. Elk diet analysis was used to identify the important seasonal forage species and then estimate the biomass of forage species. Forage species digestibility defined as percent dry matter digestibility (DMD) was estimated using sequential fiber analysis. We then estimated the nutritional resources, measured as the biomass of digestible forage (g/m^2), at each sampling site. Finally, we used spatial geographic information system covariates in statistical models to predict the landscape nutritional resources available to elk in late summer.

based on the differing landscape attributes of the winter ranges.

STUDY AREA

The 4,214 km^2 study area was located in the southern Bitterroot Valley in western Montana, USA (Fig. 2). The area encompasses the headwaters of the West Fork and East Fork of the Bitterroot River. The West Fork area consists of rugged terrain, with elevations ranging from just over 1,200 m in the valley bottom to over 3,000 m along the Bitterroot crest. The majority of the area is heavily forested, with lower elevation riparian areas and grasslands. The East Fork area consists of more moderate terrain, with elevations ranging from 1,100 m to just under 2,800 m along the Continental Divide. Throughout the study area, lower elevation areas are primarily montane grasslands, composed of Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and elk sedge (*Carex geyeri*);

and montane mixed-conifer forests, dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Higher elevation areas are predominately subalpine mesic spruce fir forests, which are dominated by lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*), and subalpine fir (*Abies lasiocarpa*). Wildfire activity is common within the study area. Large-scale wildfires occurred in 2000, 2007, 2011, and 2013, and smaller-scale fires occur annually.

Two elk populations inhabit the study area, the West Fork and East Fork populations, both of which steadily increased from 1980 to the mid-2000s. In 2004, antlerless elk harvest was deliberately increased in efforts to reduce elk populations in both areas. In the West Fork, the elk population peaked a high of 1,900 in 2005, then declined to a low of 744 elk by 2009. During this period, calf recruitment declined reaching a low of nine calves per 100 adult females in 2009. In the East Fork, the elk population peaked at a high of 4,135 in 2006, then declined to 3,332 by 2012. Calf recruitment also declined during

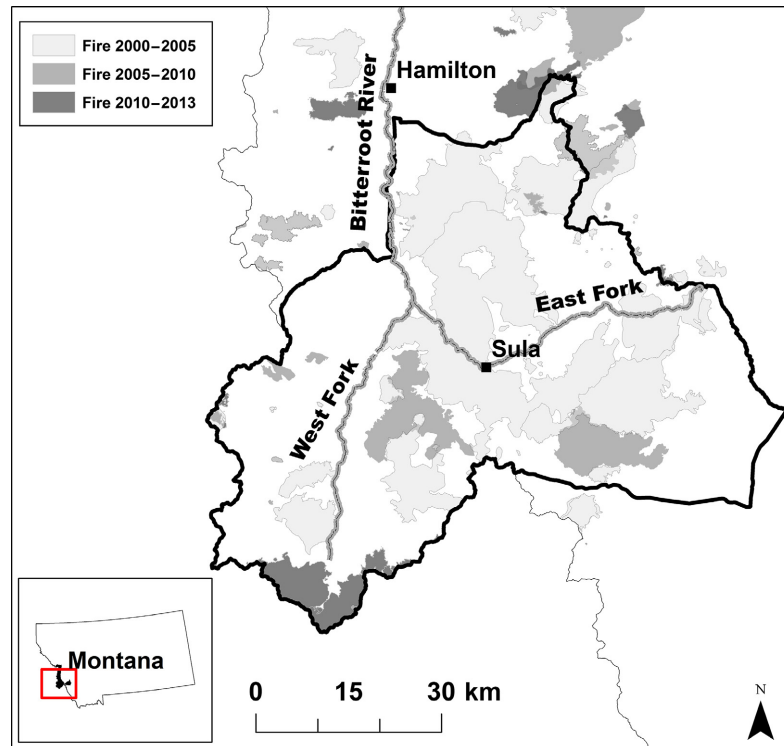


FIG. 2. The study area (black outline) containing the two elk populations (East Fork and West Fork) compared in this study located in the southern Bitterroot Valley of western Montana, USA, included lower elevation montane grassland areas and montane mixed conifer forests, as well as higher elevation subalpine and alpine forests. Large-scale wildfires burned portions of the study area during the past 15 yr.

this period, however, declines were not as severe as in the West Fork, with recruitment reaching a low of 15 calves per 100 adult females in 2009. The extent of the study area was defined by the extent of West Fork and East Fork population annual ranges, which were defined using fine-scale elk telemetry data and buffered by 5 km. There was little to no movement of female elk between these two populations. Elk are sympatric with moose (*Alces alces*), mule deer (*Odocoileus hemionus*), whitetail deer (*Odocoileus virginianus*), and bighorn sheep (*Ovis canadensis*). Wolves, coyotes (*Canis latrans*), mountain lions, and black bears (*Ursus americanus*) also occupy the study area. Mountain lions populations are at a relatively high density of 4.5 and 5.2 mountain lions/100 km² in the West Fork and East Fork, respectively, and mountain lions are the primary predator of elk in both the West Fork and East Fork populations (Eacker 2015).

METHODS

Overview

We used a combined ground and remote-sensing based approach to develop a landscape-scale summer elk nutritional resources model (Fig. 1). First, we used a ground-based approach to measure available biomass of plants

and plant phenological stage during late summer. Second, because ungulate diet selectivity may be able to compensate for differences in availability (Parker et al. 2009), we measured year-round diet composition in the two study areas using fecal plant fragment analysis. We predicted the diet of elk in the study area with higher-quality habitat would contain the greatest proportion of higher-quality plant species. Next, we estimated differences in the availability of forage (i.e., consumed plants) biomass between study areas by filtering available biomass to include only the plant species that were strongly represented in diet analysis (hereafter called forage plants). In addition to measuring available forage biomass, we sampled these forage plants in different phenological stages to estimate phenological stage-specific dry matter digestibility (DMD). Lastly, we combined phenological stage-specific forage digestibility and forage biomass availability to develop a landscape model of summer elk nutritional resources (i.e., grams of digestible forage biomass/m²; Hebblewhite et al. 2008, Pastor 2011). Ultimately, what matters for ungulate population dynamics is whether differences in nutritional resources translate to life-history traits. Therefore, we tested for the effect of summer nutritional resources in each study area on fall body condition and pregnancy rate of elk in each population.

Elk diet

We collected pellet samples to identify the important elk forage species in the summer and winter using fecal plant fragment analysis in both the East Fork and West Fork study areas. Each sample constituted a composite of 10–20 individual pellets selected at random from 10 pellet groups within a 2–5 ha area. We collected only moist samples to ensure pellets were fresh and from the season of interest. We collected a total of seven samples (3–4 in each study area) in spring (May–June), summer (July), late summer (August–September), and winter (December–March). Fecal plant fragment analyses were conducted at the Wildlife Habitat Nutrition Laboratory (Pullman, Washington, USA) at level B (>5% prevalence in diet) species composition to estimate East Fork and West Fork seasonal diets. We then ranked the top plant species consumed in the diet of elk during the summer growing season (May–September) and winter (December–March) using the species that constituted 95% of the total diet, which resulted in 22 species in both summer and winter. Although microhistological examination of plant species in feces may be biased due to different levels of digestion of each plant species, we believe our approach to include 95% of the total diet accurately captured the dominant forage species present. We used this list of forage species to screen our plant biomass data and develop models predicting nutritional resources (see Methods, Forage biomass).

To test for differences in forage plants between the East Fork and the West Fork in the different seasons, we used multivariate statistical analysis based on the percent occurrence of each species in the diet. We partitioned the variance into different groups (all combinations of East Fork/West Fork and seasons) using a between-class principal component analysis (Culhane et al. 2002). The between-class analysis is carried out by ordination of predefined groups and then projecting the individual sampled locations onto the resulting axes. We used permutation tests with 1,000 repetitions to assess the statistical significance of the between-class analysis. This statistical analysis was carried out using R library *ade4* (Chessel et al. 2004).

Forage biomass

We estimated the biomass and species composition across our study area using random plot locations within eight land cover types based on a proportional allocation sampling design (Krebs 1989). The eight land cover types included wet forests not recently burned (i.e., burned more than 15 yr prior), wet forests burned 0–5 yr prior, wet forests burned 6–15 yr prior, dry forests not recently burned, dry forests burned 0–5 yr prior, dry forests burned 6–15 yr prior, grasslands, and shrublands. Our land cover model was developed based on the environmental site potential and canopy cover (CC) land cover products from LANDFIRE (*available online*); fire history

data collected by the Bitterroot, Lolo, and Beaverhead-Deerlodge National Forests; and wetlands data from the National Wetlands Inventory (*available online*; Appendix S1).^{6, 7} Wet forests included higher-elevation subalpine and alpine forests dominated by *P. contorta*, *A. grandis*, and *A. lasiocarpa*. Dry forests included lower-elevation mixed conifer forests dominated by *P. ponderosa* and *P. menziesii*.

At each sampling site, we established a 40-m transect along the contour of the slope. At the 0-, 10-, 20-, 30-, and 40-m mark on the transect, we recorded species composition and percent cover within a 1-m² quadrat. Cover estimates were independent of each other, allowing total cover to exceed 100%. At the 0-, 20-, and 40-m quadrat, we established a 0.5-m² clip plot and collected all of the above ground biomass of graminoids, forbs, and shrubs within the clip plot. We clipped graminoids and forbs 1 cm above ground to represent the available foraging height of elk. On shrubs, we clipped all leaves and non-woody stems. We measured wet weight to the nearest gram in the field, then dried samples at 50°C in a drying oven for 48 h and measured dry weight. Based on the percent cover of graminoids, forbs, and shrubs within the clip plot, we allocated species-specific dry biomass proportional to cover across plant lifeform (e.g., shrub, forb, graminoid) and within lifeform to plant species. We then summed the estimated biomass of important forage species in the elk diet to estimate biomass of forage species (in g/m²) at each sampling site.

Forage digestibility and phenology

To evaluate the digestibility of forage plant species, we estimated the phenological stage-specific digestibility and monitored phenological stage of forage species in each study area. We first estimated percentage of dry matter digestibility of plants in the elk diet throughout the growing season (Mould and Robbins 1982, Van Soest 1982, Cook 2002). We collected samples of the forage plants, which were identified in the diet analysis, described previously, during each major phenological stage. For each forage plant species, we collected samples (≥2 cm in height) in five phenological stages (newly emergent, 1; flowering, 2; fruiting, 3; mature, 4; and cured, 5; Griffith et al. 2002, Hebblewhite et al. 2008) from 30 sites across the study area. Plant samples were stored in paper bags in a cool, dark place, then combined into one composite sample per site and dried at 50°C for 48 h. DMD was determined using sequential detergent fiber analysis (Van Soest 1982) at the Wildlife Habitat Nutrition Lab (Washington State University, Pullman, Washington, USA). For forb and shrub species known to be high in tannins, we referred to literature values to correct for tannins using a bovine serum assay (Hebblewhite 2006).

⁶ www.landfire.gov

⁷ <http://www.fws.gov/wetlands/>

We calculated DMD adjusted for tannin content using Eqs. 1 and 2 of Hanley et al. (1992); details are given in Appendix S2. We sampled 16 forage plant species and used literature values from previous studies in Banff National Park (Hebblewhite 2006) for remaining forage species to estimate phenological stage-specific DMD in the summer and winter elk diets.

To estimate variation in phenological stage of each forage species in each study area, we repeat-sampled 29 phenology plots monthly from April to October in 2012 and 2013 following methods developed by Hebblewhite et al. (2008). Phenology plots were stratified across major phenological gradients including elevation, aspect (north, south, flat), and canopy coverage (open and closed). Each plot was located within a homogenous ≥ 2.5 -ha patch to minimize edge effects, and we oriented a 100-m transect parallel to the elevational contour through the patch. We measured plant species composition and phenological stage (new, flowering, fruiting, mature, cured) within 10 permanently marked 1-m² quadrats along the transect. We used 10 plots for this sampling instead of the five used in biomass plots to increase between-visit precision of our phenological stage estimates. We then estimated the frequency distribution of each forage species in each phenological stage between 8 July and 31 August, corresponding to the same period as forage biomass estimation.

We tested for differences in DMD and phenological stage between study areas using linear models (ANOVA), because DMD and phenological stage were approximately normally distributed. First, to test for differences in DMD of our collected plant samples, we included forage classes (forb, graminoid, and shrub), phenological stage (measured using the ordinal phenological stage from 1 for new to 5 for cured), and study area (East Fork and West Fork) as predictor variables. We fit all combinations of potential interactions from main effects only to all three-way interactions. Next, we tested for study area differences in forage plants phenological stage throughout time measured in our ground phenology plots ($n = 29$). Our predictor variables for this analysis included study area, elevation, aspect class (flat, north, south), CC class (open, closed), and month following Hebblewhite et al. (2008). Again, we fit all three-way interactions and all simpler models. We selected our best models using Akaike's information criterion, AIC, in both analyses (Burnham and Anderson 2002).

Developing a landscape nutritional resources model

We developed a landscape nutrition model (sensu Hebblewhite et al. 2008) that predicted the digestible forage biomass during late summer (Fig. 2). To do this, we first estimated the biomass (g/m²) of forage species available to elk in late summer from our biomass sampling plots. Second, we estimated the phenological stage frequency distribution for each forage plant species during late summer and the DMD of each forage species

in each phenological stage. We combined the phenological stage and DMD data to estimate the weighted average DMD of each forage species in late summer. We then calculated digestible biomass by multiplying the weighted average DMD per species by biomass of the species to estimate the total biomass of digestible forage per unit area (g/m²).

We developed generalized linear models with the gamma link function for forb, graminoid, and shrub digestible biomass as a function of spatial covariates. We evaluated 10 standardized spatial covariates: vegetation cover class, elevation, slope, aspect, CC, compound topography index, hillshade, enhanced vegetation index, leaf area index (LAI), and sampling season (Appendix S3). We obtained remotely sensed measures of vegetation indices from the MODIS satellite (Pettorelli 2013). We obtained enhanced vegetation index EVI at 250-m² resolution in 16-d intervals during the growing season (MOD13Q1; Huete et al. 2002), as well as LAI at 1-km² resolution (MOD15; Myneni et al. 2002). We averaged MODIS vegetation data (EVI, LAI) annually during 1 July–31 August of 2006–2011 and then created an average value for each index because our purpose was to develop a predictive model that was not year specific. We assumed all covariates were measured without error. This assumption means that estimates of regression coefficients are more precise than they would be if we properly accounted for uncertainty in predictor variables.

We screened spatial covariates for collinearity and included only covariates with a Pearson's correlation coefficient < 0.6 and a variance inflation factor < 3.0 (Zuur et al. 2010). Because our goal was predicting digestible biomass, and not necessarily testing a priori hypotheses, we selected the top model using backwards-stepwise model selection with $P = 0.05$ as the threshold for inclusion or exclusion of predictor variables. Analyses were performed using R version 3.1.2 (R Core Team 2014). We used unstandardized coefficient estimates from the top ranked model to develop spatially explicit predictions of forb, graminoid, and shrub biomass across the study area. We developed spatial predictions at a 30-m² pixel resolution, and we ignored spatial autocorrelation in predictions. To validate the accuracy of predictive biomass models, we compared the observed and predicted graminoid, forb, and shrub biomass values using a general linear model and report R^2_{adj} values.

Linking landscape models of nutritional resources to ungulate responses

We used elk location data collected from collared adult female elk to estimate seasonal population ranges, then compared seasonal elk distribution to the landscape nutrition model, and investigated whether differences in body condition and pregnancy rates were associated with differences in elk access to digestible forage biomass. Elk were captured using helicopter net gunning or chemical immobilization in compliance with the University of

Montana animal handling and care policy # 027-11MHWB-042611. We collared elk with Global Positioning System radiocollars programmed to collect 12–24 locations per day. We used location data collected from 8 July to 31 August to estimate a population-level summer utilization distribution and data collected from 1 January to 31 March to estimate a population-level winter utilization distribution. We estimated population-level seasonal ranges for East Fork and West Fork elk as the 90% fixed-kernel isopleth, calculated using the reference bandwidth (Worton 1989). We used these seasonal ranges to estimate seasonal, population-level digestible forage biomass to test for differences in digestible forage biomass available to elk in each population and season.

We then evaluated the effects of population differences in seasonally available digestible forage biomass on body fat, pregnancy rates, and the link between these two indicators of nutritional condition. We sampled elk from the East Fork and West Fork populations during the late fall (26 November–4 December) and late-winter (1 February–18 February). Sampling occurred simultaneously (i.e., within 48 h) in both populations. Different individuals were sampled during each season and year. During capture, we collected a blood sample to determine pregnancy status based on pregnancy specific protein-B levels, and we aged elk based on tooth eruption patterns. We measured chest girth and assessed body condition using a portable ultrasound machine to estimate levels of ingesta-free body fat (IFBF) that, following the revised methods of Cook et al. (2010), included an allometrically scaled MAXFAT index. During fall captures, we assessed lactation status based on the presence of milk in the udder, presence of saliva on the udder, and overall udder size. During late-winter captures, we could not determine if elk had lactated the previous summer and fall, so we did not estimate lactation status.

We first tested for effects of population (East Fork or West Fork) and year (2012, 2013) on fall IFBF while controlling for lactation status (yes, no) using a linear model (i.e., ANOVA). We fit all potential combinations of variables (from the full factorial down) and selected the top model explaining IFBF using AIC corrected for small sample sizes, AIC_c (Burnham and Anderson 2002). Next, we tested for effects of IFBF, population, age class, and year on pregnancy rate using a logistic regression model (Hosmer and Lemeshow 2000). We classified age class as prime age (age 2–9) or older age (10+). We did not consider season (early, late winter) nor lactation status in the analysis of pregnancy rates because lactation status was unknown in late-winter samples and because preliminary analyses confirmed that pregnancy rates increased by late winter, which was biologically impossible and likely a sample size artifact (*unpublished data*). We fit models with the main effect of IFBF, population, and year, and all possible 2 and 3-way interactions and selected the top model explaining variation in pregnancy using AIC_c .

RESULTS

Elk diet

We processed 55 composite samples of elk diet. Elk summer diet included 72 species and was twice as diverse as the winter diet that included only 34 species. A total of 22 species comprised 95% of the summer diet and were considered summer forage species, and 22 species comprised 95% of the winter diet and were considered winter forage species (Appendix S4). Despite overall forage class composition similarity, there were important differences in species composition in East Fork and West Fork elk diets.

The between-class analysis of the study area/season effect indicated that elk diet was significantly different between the sampling periods and the two regions (between class inertia observed = 0.217, inertia simulated = 0.130, $P < 0.001$). Projecting the different groups onto the components shows the degree of variability of the diet composition in each of the eight classes (Fig. 3). The largest between-class differences in diet at the plant species level occurred in winter. Component 1 (CS1) was positively associated mainly with winter pellet samples collected in the East Fork (class normed score, $RS1 = 2.09$) and the West Fork ($RS1 = 1.40$; Fig. 3; Appendix S4) and negatively associated with samples collected in late summer in West Fork ($RS1 = -1.06$). Component 2 (CS2) was positively associated mainly with samples collected in winter in the East Fork ($RS2 = 1.99$), but negatively associated with winter samples from the West Fork ($RS2 = -1.93$).

The contrast between the two study areas in winter diet (Figs. 3 and 4) was predominantly driven by the forage plant species *Linnaea borealis* ($CS1 = 0.37$, $CS2 = -0.58$), *Carex* spp. ($CS1 = 0.11$, $CS2 = -0.30$), *Phleum alpinum* ($CS1 = 0.23$, $CS2 = -0.31$), and *Danthonia* spp. ($CS1 = 0.29$, $CS2 = 0.18$), which were associated with winter diet in the West Fork (Fig. 4; Appendix S4). In contrast, *Festuca altaica*/*campestris* ($CS1 = 0.24$, $CS2 = 0.36$), *Muhlenbergia cuspidata* ($CS1 = 0.26$, $CS2 = 0.32$), and *P. spicata* ($CS1 = 0.23$, $CS2 = 0.25$) were good discriminators for diet samples collected during winter in the East Fork. Additional forage species that had comparatively high loadings were *F. idahoensis* ($CS1 = 0.40$) and *Lupinus* spp. ($CS1 = -0.32$) on component 1 during summer (Fig. 4). In spring, elk in the East Fork consumed more *Pseudoregenaria*, *Balsamorhiza sagittata*, *Festuca* spp., and *Mahonia repens* (leaf), while consuming less *Carex* spp., *Pinus*, and *Poa* than West Fork elk (Fig. 4), and these differences continued in summer. By late summer, West Fork elk consumed more cured *Balsamorhiza*, whereas East Fork elk consumed double the *Lupinus* in July–September and 8% *Xerophyllum tenax* compared to 0% in the West Fork (Appendix S4).

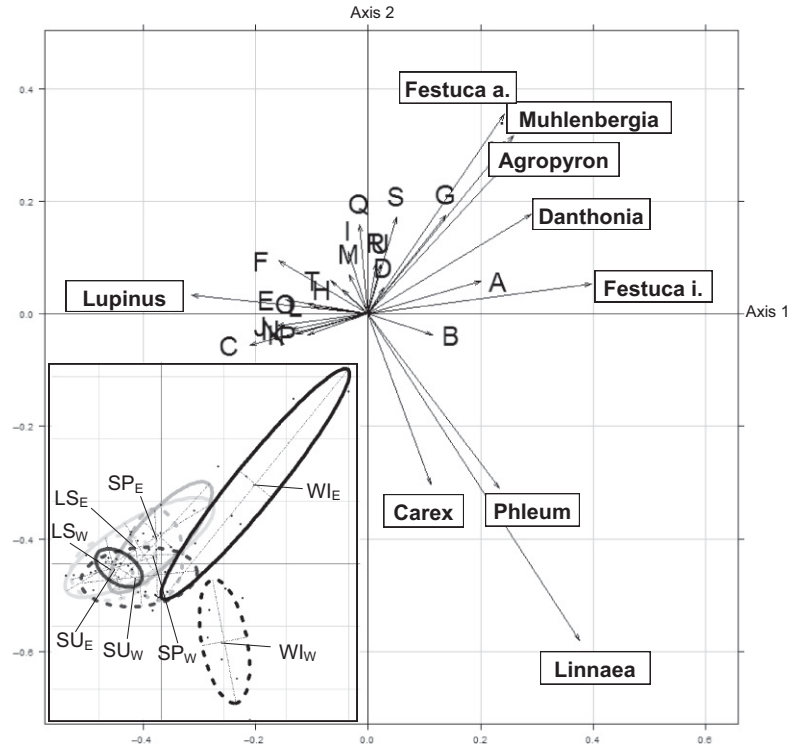


FIG. 3. Between-class analysis based on forage plant species composition in elk feces using eight groups composed of four seasons (Wi, winter; Sp, spring; Su, summer; LS, late summer) and two elk populations (E, East Fork; W, West Fork) in the southern Bitterroot Valley of western Montana, USA, 2012–2013. Points in the smaller inset graph represent each fecal sample positioned according to its score value on the two axes of the between-class analysis, highlighting that the biggest differences in diet occurred in winter. The large graph shows how each of the forage species contributed to the first two components, revealing, for example, that during winter, forage species composition differed the most from *Festuca* in the East Fork to *Carex* spp. and *Linnaea borealis* in the West Fork. The proximity between the different season and study area groups is linked to their similarity in forage species composition.

Elk forage biomass, digestibility, and phenology

We sampled vegetation at a total of 235 sites during 8 July–31 August, 2012–2013 (Appendix S5). The biomass of summer and winter forage forbs was highest in the wet forests burned more than 15 yr prior (Table 1; Appendix S6). The biomass of summer and winter forage graminoids was highest in the grasslands. The biomass of summer forage shrubs was highest in wet forests burned 6–15 yr prior. Forage abundance in both the wet forest and dry forest cover class decreased 0–5 yr post fire, reached a peak 6–15 yr post fire, and then slowly declined more than 15 yr post fire. Forage shrub biomass was low within the shrubland land cover class because this cover class was primarily sagebrush-steppe and contained little of the shrub species that elk consume. The biomass of winter forage shrubs was low across all cover classes.

We collected an average of 6.4 DMD samples per species per phenological stage from 16 species in 5 phenological stages. DMD varied across species and phenological stage and was higher in forb and shrub species as compared to graminoid species (Table 2). For our first analysis of differences in % DMD, the top model explaining % DMD did not contain any effect of study area confirming no species-specific differences in % DMD between study areas.

In the top model for % DMD, there were predictable differences in % DMD by forage class ($F_{\text{class}} = 35.0$, $p < 0.001$) with forbs on average highest, followed by shrubs and graminoids (Table 2). Early phenological stages had higher % DMD ($F_{\text{phase}} = 23.5$, $p < 0.001$), but few of the 2-way interactions between class and stage were significant ($F_{\text{class:stage}} = 2.48$, $p = 0.01$). The closest second ranked model with the full 3-way interaction between study area, forage class and phenological stage had a $\Delta\text{AIC} = 13.4$ and 30 parameters, only 15 of which had 95% confidence intervals that did not overlap 0. Main effects of area ($F_{\text{area}} = 0.82$, $p = 0.36$) and area:class ($F_{\text{area:class}} = 1.19$, $p = 0.30$) and area:stage ($F_{\text{area:stage}} = 1.16$, $p = 0.32$) interactions were not significant in this second-ranked model. Therefore we interpret there to be no difference in species-specific DMD between our two study areas.

Our analysis of differences in plot-level plant phenological stage based on phenological scores also revealed no differences between East Fork and West Fork. The top model did not contain an effect of study area (see Appendix S7), and plant phenological stage was predictably affected by month (increasing phenological stage of $\beta = 0.57$ per month, $P < 0.001$), elevation (decreasing phenological stage of $\beta = -0.3$ per 1,000 feet of elevation gain, $P = 0.0005$), was earlier in open

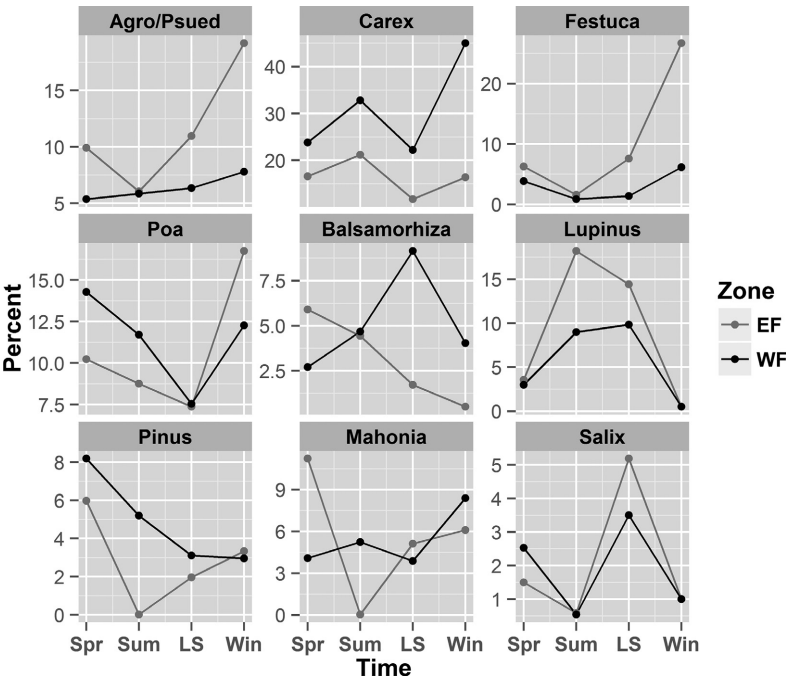


FIG. 4. Forage plant species composition in the diet of elk in the East Fork (EF) and West Fork (WF) of the southern Bitterroot Valley of western Montana, USA, 2012–2013, as a function of phenological period during the growing season (Spr, spring; Sum, summer; LS, late summer), and winter (Win). Species names correspond to Appendix S4.

TABLE 1. The mean biomass of summer and winter forb, graminoid, and shrub forage species for elk in different land cover types in the southern Bitterroot Valley of western Montana, USA, during 2012–2013.

Landcover	Summer forage species			Winter forage species		
	Forb biomass (g/m ²)	Graminoid biomass (g/m ²)	Shrub biomass (g/m ²)	Forb biomass (g/m ²)	Graminoid biomass (g/m ²)	Shrub biomass (g/m ²)
Shrubland	4.7	16.2	0.7	4.6	20.4	0.1
Grassland	7.8	30.8	10.5	5.1	35.4	1.5
Wet forest, burn age 1–5	11.2	2.1	2.6	0.0	2.1	0.0
Wet forest, burn age 6–15	22.1	18.3	22.4	3.1	19.7	0.2
Wet forest, burn age > 15	22.8	9.4	20.7	2.4	10.0	0.6
Dry forest, burn age 1–5	6.6	7.2	2.0	1.2	7.4	0.9
Dry forest, burn age 6–15	20.7	16.3	16.4	6.0	16.4	1.4
Dry forest, burn age > 15	12.3	15.2	9.5	8.1	15.6	1.6
Average	14.4	17.7	13.2	4.4	19.7	0.9

TABLE 2. The average percent dry matter digestibility of forb, graminoid, and shrub forage species in the diet of elk in the southern Bitterroot Valley of western Montana during 2012–2013 by phenological growth stage.

	New	Flowering	Fruiting	Mature	Cured	Average
Forb	75.7	71.7	76.0	75.6	64.5	73.7
Graminoid	70.5	65.6	70.2	69.2	64.0	67.6
Shrub	78.0	69.2	70.9	62.6	63.7	71.2

Note: Phenological stages were defined as newly emergent, flowering, fruiting, mature, and cured.

canopied habitats ($\hat{\beta} = 0.6$, $P < 0.001$), was delayed in north aspects ($\hat{\beta} = -0.47$, $P = 0.004$), and was earlier in 2013 ($\hat{\beta} = -0.8$, $P < 0.001$). There were also no phenological stage differences when we broke plants into forage class (Appendix S7). Although study area was retained in the top graminoid and shrub model, effects

TABLE 3. The summer and winter nutritional resources, measured as grams of digestible matter per m², by landcover type in the East Fork (EF) and West Fork (WF) seasonal elk ranges in the southern Bitterroot Valley of western Montana during 2012–2013.

Cover Type	Summer						Winter					
	Forb		Graminoid		Shrub		Forb		Graminoid		Shrub	
	EF	WF	EF	WF	EF	WF	EF	WF	EF	WF	EF	WF
Grassland	7.5	4.0	32.0	10.1	13.8	8.0	5.8	4.5	31.9	9.6	5.0	2.9
Shrubland	3.6	2.0	13.4	13.5	8.0	1.0	3.5	2.0	12.8	12.5	2.0	–
Dry Forest – Burn Age 0–5	–	5.4	–	6.4	–	1.6	–	3.5	–	6.3	–	1.3
Dry Forest – Burn Age 6–15	11.9	13.8	17.2	5.8	14.8	10.3	7.2	2.5	16.0	5.0	2.0	3.5
Dry Forest – Burn Age > 15	16.1	4.9	13.9	9.6	7.9	5.9	11.2	5.5	13.1	8.9	3.2	1.4
Wet Forest – Burn Age 0–5	–	9.6	–	2.6	–	1.6	–	0.0	–	2.6	–	–
Wet Forest – Burn Age 6–15	14.3	–	12.7	–	14.6	–	4.2	–	12.3	–	1.3	–
Wet Forest – Burn Age > 15	14.6	13.3	7.6	9.5	14.4	6.4	3.3	0.5	7.1	8.8	3.5	0.0

were non-significant or very weak (graminoid $\hat{\beta}_{WF} = -1.40$, $P = 0.154$; shrub $\hat{\beta}_{WF} = 0.277$, $P = 0.015$). Thus, we conclude that there are few differences in plant-level phenological stage between study areas.

Landscape nutritional resources model

Despite no support for differences in DMD between plant samples or in phenological stage based on ground plots in the East Fork and West Fork study areas, nutritional resources (measured as grams of digestible forage biomass/m²) varied across land cover types throughout the study area and between study areas as a function of differences in land cover (Table 3). On average, summer herbaceous nutritional resources was highest in wet forests burned 6–15 yr prior and grasslands. Summer shrub nutritional resources was highest in wet forests burned 6–15 yr prior, and wet forests burned more than 15 yr prior (Table 3). Winter herbaceous nutritional resources were highest in grasslands and shrublands, and winter shrub nutritional resources were highest in grasslands. Within landcover classes, graminoid, and shrub nutritional resources were higher in the East Fork than the West Fork. Forb summer nutritional resources differed between the East and West Fork, with quality higher in some East Fork areas and higher in some West Fork areas (Table 3).

The best model of summer forb nutritional resources explained 26% of the variation in nutritional resources, and landcover type, season and elevation were the strongest predictors of nutritional resources (Table 4, Fig. 5). The best model of summer graminoid nutritional resources explained 37% of the variation in nutritional resources, and landcover type and LAI were the strongest predictors of nutritional resources. The best model of summer shrub nutritional resources explained 19% of the variation in nutritional resources, and landcover type and aspect were the strongest predictors of nutritional resources.

The top ranked model of winter forb nutritional resources explained 26% of the variation in nutritional resources, and landcover type and aspect were the strongest predictors of nutritional resources (Table 4, Fig. 5). The top ranked model of winter graminoid nutritional resources explained 37% of the variation in nutritional resources, and landcover type and LAI were the strongest predictors of nutritional resources. The top ranked model of winter shrub nutritional resources explained 19% of the variation in nutritional resources, and canopy cover and EVI were the strongest predictors of nutritional resources.

Linking landscape nutritional resources models to ungulate responses

Summer range location data were collected from 60 individual elk in the East Fork and 44 individual elk in the West Fork. The East Fork summer range was 1,441 km² and the West Fork summer range was 519 km². A greater proportion of the East Fork summer range was composed of forests burned 6–15 yr prior, and a greater proportion of the West Fork range was composed of recently burned forests or forests not burned within 15 yr (Table 5). The East Fork summer range had higher mean digestible forb, graminoid, and shrub forage biomass (23.3, 44.8 and 8.7 g/m², respectively) than the West Fork summer range (18.5, 20.1 and 8.3 g/m²), and the difference in digestible forage biomass was greatest for graminoids.

Winter range location data were collected from 66 individual elk in the East Fork and 50 individual elk in the West Fork. The East Fork winter range was 353 km² and the West Fork winter range was 244 km². The East Fork winter range was composed of a higher proportion of grasslands and forests burned 6–15 yr prior, and the West Fork winter range was composed of a higher proportion of forests not burned within the past 15 yr (Table 5). The East Fork winter range had higher

TABLE 4. Standardized coefficient estimates for top models explaining the variation in summer and winter forb, graminoid, and shrub nutritional resources available to elk in the southern Bitterroot Valley of western Montana during 2012–2013.

	Summer			Winter		
	Forb	Graminoid	Shrub	Forb	Graminoid	Shrub
(Intercept)	1.31	2.11	−0.69	0.75	2.22	1.16
EVI	0.37	0.34	0.00	–	0.34	0.38
LAI	0.05	−0.74	0.00	−0.20	−0.79	0.13
Wet Forest† – Burn Age 1–5	−0.18	−1.48	−2.18	–	−1.10	–
Wet Forest – Burn Age 6–15	0.22	0.84	0.33	−0.29	0.74	–
Dry Forest – Burn Age > 15	−0.18	0.34	−0.57	1.02	0.28	–
Dry Forest – Burn Age 1–5	−0.87	−0.49	−2.30	−0.19	−0.43	–
Dry Forest – Burn Age 6–15	0.72	0.68	−0.09	1.09	0.58	–
Shrubland	−0.68	0.36	−3.08	0.40	0.19	–
Grassland	−0.17	0.74	0.03	0.40	0.72	–
CTI	−0.20	0.27	–	−0.40	0.24	−0.25
Aspect South	0.37	−0.50	2.36	−0.51	−0.51	−0.39
Elevation	0.60	−0.19	–	0.24	−0.16	–
Hillshade	0.19	−0.04	0.00	0.07	−0.06	−0.17
Season	0.66	0.28	–	0.46	0.31	−0.37
Slope	0.11	0.21	−0.01	0.16	0.14	−0.20
Canopy Cover	−0.06	−0.09	0.01	−0.52	−0.07	−0.46
Aspect North	–	−0.42	2.18	−0.92	−0.47	–

Notes: Boldface values denote a value with a confidence interval that does not include 0. Abbreviations are CTI, compound topography index; EVI, enhanced vegetation index.

†The base landcover type was Wet Forest – Burn Age > 15 years.

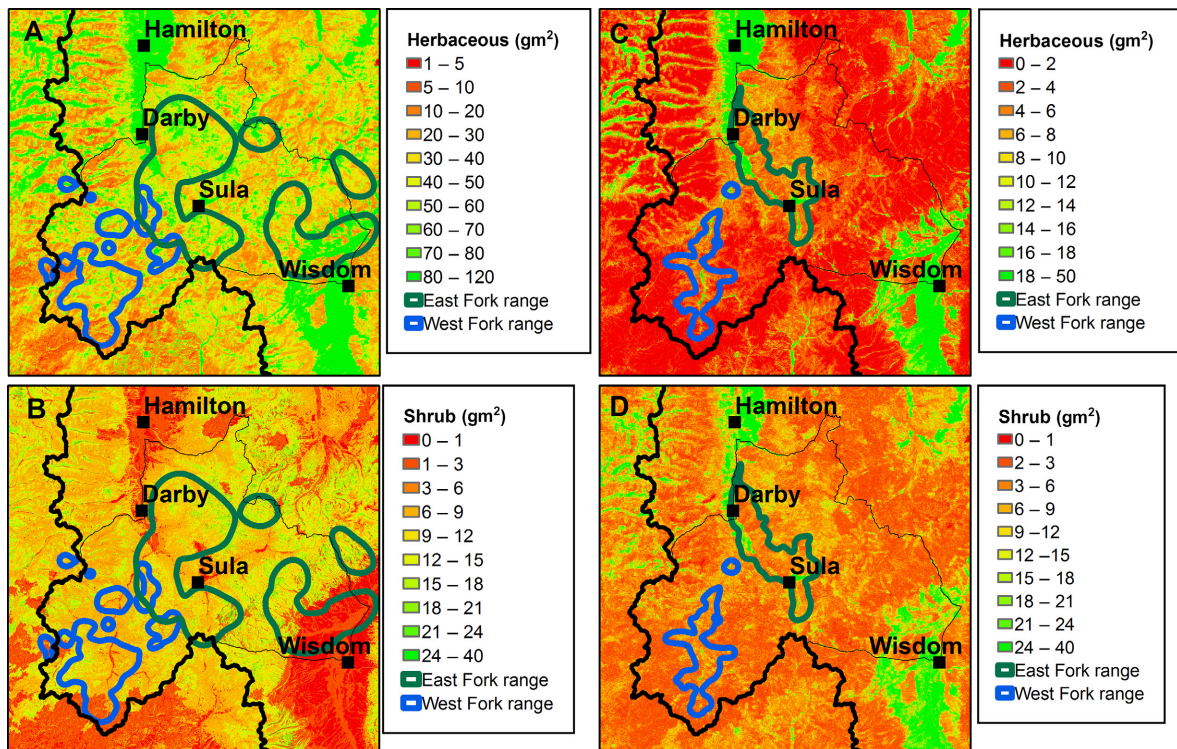


FIG. 5. The estimated (A, B) summer and (C, D) winter herbaceous and shrub nutritional resources (in grams of digestible matter/m²) in the East Fork and West Fork elk seasonal ranges in the southern Bitterroot Valley of western Montana, USA, as predicted from top ranked summer and winter landscape nutritional resources models.

TABLE 5. The percentage of the East Fork (EF) and West Fork (WF) seasonal elk ranges comprised of each land cover type in the southern Bitterroot Valley of western Montana, USA, 2012–2013.

Cover type	Summer range		Winter range	
	EF	WF	EF	WF
Shrubland	9.6	<1	2.8	<1
Grassland	26.9	21.5	54.6	30.8
Wet forest, burn age 0–5	2.5	5.7	0.0	0.8
Wet forest, burn age 6–15	18.5	5.5	2.3	1.2
Wet forest, no recent burn	15.9	16.6	0.2	4.8
Dry forest, burn age 0–5	2.9	8.5	0.1	3.5
Dry forest, burn age 6–15	15.9	10.4	25.8	11.3
Dry forest, no recent burn	8.0	31.7	14.2	47.6

digestible forb, graminoid, and shrub forage biomass (2.9, 22.0, and 2.4 g/m², respectively) than the West Fork winter range (1.6, 7.5, and 2.1 g/m², respectively), and the difference in biomass was greatest for graminoids.

The top model explaining variation in fall IFBF included population, lactation status, and year, and all interactions ($F_{7,29} = 5.86$, $P = 0.0003$, $R^2_{\text{adj}} = 0.49$). West Fork elk, on average, had 2.4% lower IFBF ($\hat{\beta}_{\text{WF}} = -2.41$, $P = 0.046$) than East Fork elk (Fig. 6). Lactation reduced body fat on average by 2.0% ($\hat{\beta}_{\text{Status}} = -2.00$, $P = 0.101$). In 2013, all elk had 1.0% higher body fat ($\hat{\beta}_{2013} = 1.06$, $P = 0.454$), and non-lactating West Fork elk had 4.6% higher body fat ($\hat{\beta}_{\text{WF} \times 2013} = 4.59$, $P = 0.015$). The most important comparison showed that as expected, fall IFBF of lactating elk was higher in the East Fork than in the West Fork in both 2012 and 2013 (i.e., there was no significant interaction between population \times status, $P = 0.410$). Mean body fat for lactating elk in the West Fork was 6.3% in 2012 and 7.1% in 2013. Mean body fat for lactating elk in the East Fork was 7.1% in 2012 and 7.5% in 2013. The interaction between population, lactation status, and year was marginally significant, indicating a difference in IFBF for lactating and non-lactating

elk in the West Fork in 2013 ($\hat{\beta}_{\text{WF} \times 2013 \times \text{status}} = -4.27$, $P = 0.120$).

Overall, East Fork elk pregnancy rate was higher than West Fork pregnancy rate in 2011, 2012, and 2013, averaging 89% ($n = 65$) as compared to 72% ($n = 53$) in the West Fork (Fig. 7A). The top model explaining pregnancy rate was a function of population and IFBF; the second ranked model which was a function of population, IFBF, and age class had a ΔAIC of 1.30; the third ranked model, which was a function of population, IFBF, and the interaction had a ΔAIC of 1.65; the fourth ranked model contained only a strong effect of IFBF ($\Delta\text{AIC} = 1.98$); and no other models received support ($\Delta\text{AIC} > 4$). Based on the top model, pregnancy rate increased most strongly as a function of IFBF (Fig. 7B). For every increase of one percentage point of IFBF, the odds of becoming pregnant increased by 1.34 ($\hat{\beta} = 0.30$, z value = 2.45, $P = 0.01$). However, overall pregnancy rates were lower in the West Fork compared to the East Fork ($\hat{\beta} = -1.03$, z value = -1.96 , $P = 0.05$), indicating an additive reduction in pregnancy rates in the West Fork over and above the effects of IFBF (Fig. 7B). At an IFBF of 8%, West Fork elk had a lower probability of being pregnant (0.78) compared to East Fork elk (0.89). Age class was not included in the top ranked model and the estimated coefficient for age class in the second ranked model had a confidence interval that overlapped 0, together indicating age class had little effect in pregnancy rate, at least in these populations.

DISCUSSION

We found support for our predictions that the elk population exposed to lower summer range nutritional resources had lower nutritional condition entering winter, which resulted in lower pregnancy rates compared to the elk population exposed to higher nutritional resources. These results are consistent with recent studies linking ungulate summer range nutrition, fall body condition, and pregnancy rates (Cook et al. 2013), and

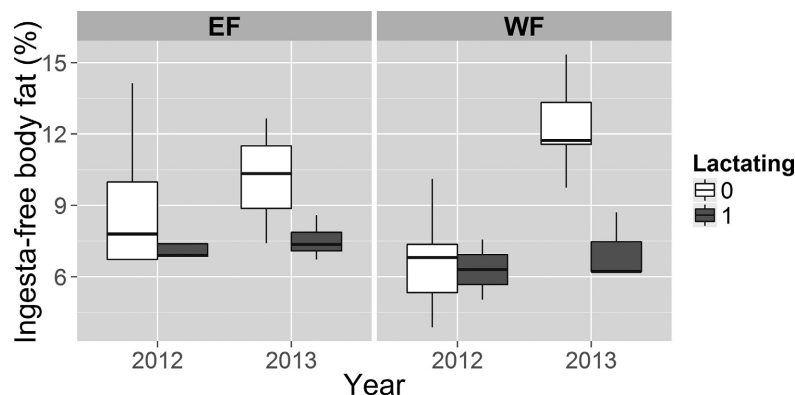


FIG. 6. The estimated fall body fat (%) of lactating (yes = 1) and non-lactating (no = 0) adult female elk in the East Fork (EF) and West Fork (WF) populations in the southern Bitterroot Valley of western Montana during 2012–2013.

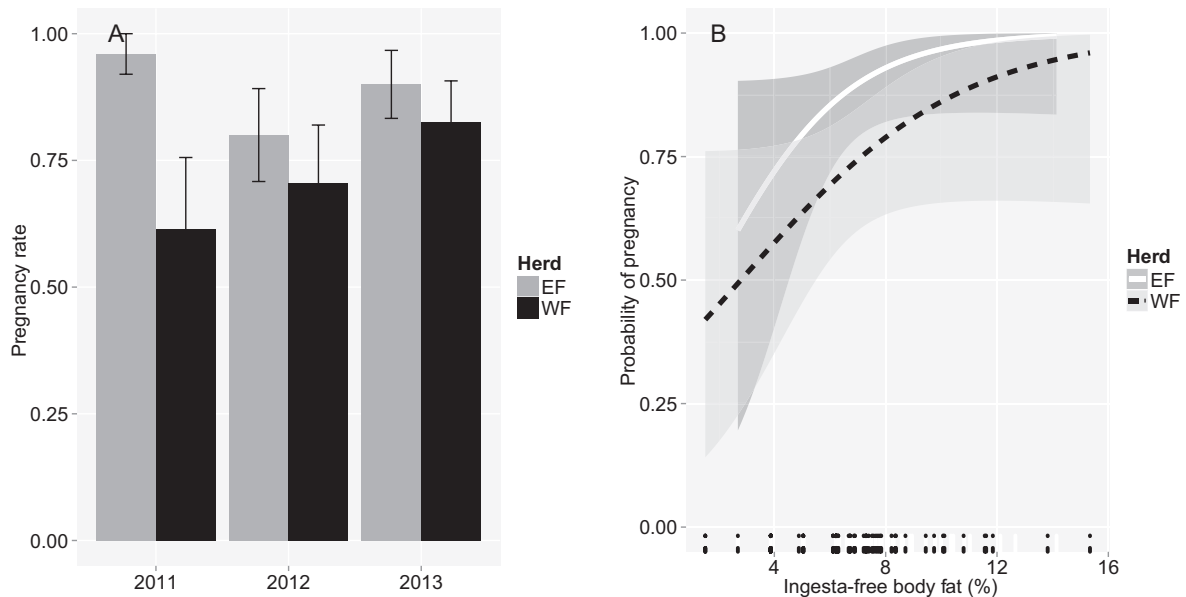


FIG. 7. The (A) average pregnancy rates of adult female elk during winter 2011, 2012, and 2013 and (B) probability of an adult female elk being pregnant as a function of the percentage of ingesta-free body fat during winter in the East Fork (EF) and West Fork (WF) populations in the southern Bitterroot Valley of western Montana, USA. Error bars represent ± 1 SE.

highlights the role of bottom-up processes in limiting ungulate vital rates and population performance. While the effects of predation on ungulate populations has been broadly studied and discussed, nutritional limitations play a less evident role in the relationship between predator and prey. Nutritional limitations on elk summer range that limit pregnancy rates and calf production may predispose populations to be more sensitive to the effects of predation. For example, Middleton et al. (2013a) showed that elk calf recruitment in eastern Yellowstone was declining potentially because of climate-change induced declines in the length of the growing season on summer range. These bottom-up effects and the interaction with predation are elemental in understanding the relative role of top-down and bottom-up factors affecting ungulate populations (Melis et al. 2009, Andren and Liberg 2015). In our study area, predation was a strong factor limiting elk calf survival and recruitment (Eacker 2015). In areas such as these experiencing carnivore recovery or high carnivore densities (Proffitt et al. 2015), the effects of nutritional limitation may be particularly important because calf production is limited. Identifying these areas and proactively managing these populations by reducing human-harvest pressure or carnivore densities, or improving habitat, may be necessary to maintain stable ungulate populations.

Our results support the previously documented relationship between body fat and pregnancy rate (Cook et al. 2013) and provide estimates linking measurements of summer range nutritional resources to observed levels of body fat and pregnancy rate for free-ranging elk. Although measurements from only two populations reported here do not alone establish a universal

nutritional-resources-pregnancy-rate relationship, these results will begin to establish a quantitative measure of nutritional resources that managers may target in efforts to provide adequate levels of nutritional resources to achieve elk population objectives. As compared to lactating elk in other parts of western North America, lactating elk in our study area had relatively low levels of body fat (in the lower 33% percentile) indicating West Fork and East Fork summer ranges had relatively low levels of nutritional resources as compared to other areas within the region (Cook et al. 2013). In spite of relatively low levels of body fat, elk pregnancy rates in the East Fork population were relatively high and did not suggest nutritional limitations, which may be related to fall precipitation and vegetation regrowth that affected short-term nutrition and ovulation (Cook et al. 2013). Additionally, the higher elk density in the East Fork population combined with the higher lactating elk fall body fat and the higher overall pregnancy rates in the East Fork population support our findings of higher levels of nutritional resources in the East Fork. Inferences based on non-lactating elk body fat levels are weak, as non-lactating elk represent a heterogeneous group of elk that did not reproduce or reproduced but lost the calf at some point in the lactation period, and thus body fat levels of non-lactating elk are not as tightly coupled with levels of available nutrition as lactating elk that consistently experience the energetic demands of lactation (Cook et al. 2004, 2013). Beyond the nutritional resources and body fat effects on pregnancy, our results also suggest underlying differences in the probability of pregnancy given comparable body fat between the two populations. These results are similar to a regional analysis of

body-fat–pregnancy relationships for 21 elk populations across four ecoregions that also documented variability in the probability of pregnancy given body fat (Cook et al. 2013). Although these results could be interpreted as evidence for predation risk effects on elk pregnancy rate (Creel et al. 2007, but see White et al. 2011, Boonstra 2013, Middleton et al. 2013b), this is unlikely given that density of the primary elk predator in this system, mountain lions, is higher in the East Fork area than the West Fork area (Eacker 2015, Proffitt et al. 2015). A more likely explanation is that the reduced probability of pregnancy represents a reproductive pause in response to chronically inadequate nutrition resources (Cameron 1994, Stewart et al. 2005, Festa-Bianchet and Côté 2008, Cook et al. 2013). Such reproductive pauses in response to nutritional stress may enhance long-term reproductive performance in ungulates (Testa 2004).

We found that the greatest differences in nutritional resources and diet composition occurred during winter, which highlights the variability in winter range nutritional resources between two geographically close areas. Nutritional conditions on winter range may affect changes in rate of body fat depletion overwinter and the probability of overwinter survival (Cook et al. 2004). The effects of these differences in winter nutrition are difficult to assess, as comparisons of late-winter body fat data are affected by summer/autumn nutritional condition and the proportion of the population that lactated during the summer and fall (Cook et al. 2004, 2013). Our late-winter body fat data suggest that elk in the West Fork were in poor nutritional condition (*unpublished data*, this study). While this is in part due to the lower quality summer range forage, the lower quality winter range forage may have resulted in additional declines in body fat as compared with elk wintering in areas of higher quality winter forage. However, because we sampled different individuals during fall and late-winter, we were unable to assess potential differences in overwinter body fat depletion. Lower quality forage on winter range has the potential to affect reproductive performance and population demographics in several ways (Raedeke et al. 2002). Winter range nutrition may affect overwinter survival of juvenile or adult ungulates (Cook et al. 2004, Bishop et al. 2009). Additionally, the female may devote less energy to gestation if she is nutritionally stressed, potentially resulting in lower calf birth weight (Carstens et al. 1987). Calf birth weight is an important predictor of neonate calf survival (Griffin et al. 2011). Therefore, while summer nutrition may affect pregnancy rate and overwinter survival rate, it is important to also recognize that winter nutrition may affect calf birth weight and neonate survival the following spring or overwinter survival during the current winter. Therefore, biologists should consider that both summer and winter nutritional resources affect population dynamics but in different ways.

Summer range nutritional resources, as indexed by our measure of digestible forage biomass, are the result of

forage species abundance (i.e., biomass), DMD, and phenological stage. A strength of this approach is that it incorporates both forage species digestibility and availability, allowing for the effects of fire or other disturbances on nutritional resources to be better understood and used to inform habitat management decisions (i.e., determine if plant species composition, forage digestibility, or a combination of these factors are associated with the disturbance). However, this index of nutritional resources has the potential to underestimate the important effects of forage digestibility on animal performance. For example, a high availability of species with low to average digestibility could result in an overall high value of digestible biomass, which could be misleading as the important effects of high forage quality based on digestibility on the performance of lactating female elk is well documented (Cook et al. 2004). Thus, our metric has the potential to identify areas with high sub-optimal forage digestibility as high in nutritional resources if a high abundance of low quality forage species are available. Several other measures of ungulate nutritional resources that explicitly account for forage quality has been employed in other studies (see Hobbs and Swift 1985, Coughenour and Singer 1996, Moen et al. 1997), and although no standard exists, we recommend metrics of digestible forage biomass, or biomass of forage species of a given digestibility levels (Hobbs and Swift 1985), as a metric to inform ungulate habitat management decisions.

On the summer ranges within our study area, we found similarity in the species of plants that elk consumed. These diet results based on microhistological analysis may have underestimated the occurrence of more digestible forage species due to the differences in levels of digestion or may reflect a lack of the availability of more highly digestible forage species. Additionally, the digestibility of forage species and the phenological stage of forage species were similar between the summer ranges within our study area, suggesting that the differences in summer range nutritional resources were likely less related to overall differences in summer diet, plant digestibility, or plant phenological stage, and more likely related to the recent fire history that affected land cover composition and forage abundance on the two summer ranges (Turner et al. 1994a, Kie et al. 2003, Fisher and Wilkinson 2005). Although both areas have experienced significant wildfire activity, a higher proportion of the East Fork summer range was burned 6–15 years ago, the period during which forage abundance and quality is highest. The West Fork summer range experienced more fire activity during the past five years, and these were high-severity fires that resulted in little vegetation regrowth. Additionally, nearly 32% of the West Fork summer range was composed of dry forest that had not burned in the past 15 years. The biomass of forbs in this land cover type is reduced as compared to similar forests burned in the past 6–15 years, and this important difference in the abundance of forbs likely accounts for

some of the differences in overall summer nutritional resources between the areas. Our results echo previous studies that showed the strongest effect of fire on landscape forage availability for large herbivores is caused by changing the land cover composition from forested to burned forests and the corresponding shifts in plant communities to more herbaceous and nutritious vegetation (Sachro et al. 2005). For example, in the Rocky Mountains of Banff National Park, burning coniferous forests led to the biggest increases in post-fire herbaceous forage biomass from 146 to 790 kg/ha, consistent with the scope of biomass differences we report here in the Bitterroot (Sachro et al. 2005). Similarly, in winter in Yellowstone's Northern Range following the 1988 fires, burned coniferous forests had 368 kg/ha more available biomass than unburned stands (Turner et al. 1994b, Wallace et al. 1995, Smith 2000).

Wildfires have landscape-scale effects on ungulate forage and potentially ungulate productivity (Turner et al. 1994a, Romme et al. 2011). Decades of fire suppression resulting in forest maturation and a more closed canopy may have reduced ungulate nutritional resources and population carrying capacity. The large-scale wildfires within our study area that occurred in 2000, 2007, 2011, and 2013 likely resulted in short-term declines in ungulate nutritional resources. This period was likely followed by a period of increasing forage quantity and quality, largely due to changes in land cover composition. While some previous studies have demonstrated short-term effects of fire increase quality of forage plants through increased nitrogen mineralization (Hobbs and Spowart 1984, Tracy and McNaughton 1997, Greene et al. 2012), these positive effects of fire are often very short lived (i.e., <2–3 years; Hobbs and Spowart 1984) and commonly confounded with fire-induced delays in plant phenological stage that improve nutritional resources (Bork et al. 2002). However, in our study, we found no differences in phenology scores between burned and unburned sites 6–15 years later, nor between burn/unburned and study areas (*unpublished data*). Instead, it seems that the emerging consensus, consistent with our landscape-scale assessment, is that fire has perhaps the greatest effect on ungulates through changes to overstory vegetation and by shifting plant communities to earlier seral stages (Turner et al. 1994a, Kie et al. 2003). Ungulate selection for emergent vegetation in recently burned areas is well documented (Hobbs and Spowart 1984, Allred et al. 2011, Greene et al. 2012), and such selection may be due to changes in plant composition of favored forage plants, short-term increases in nutritional resources post-fire, and/or increases in herbaceous biomass. Additional and more focused sampling across fire distributions and histories is needed to understand the relationship between time since fire and nutritional resources, and how fire severity and land cover type affect these relationships. Further, given the increased prevalence of prescribed fire for management, more detailed research contrasting wildfire and prescribed fire effects

on forage abundance and quality would help to develop recommendations regarding the timing and location of prescribed fires implemented to benefit ungulates.

Scaling up from the plant and plot-level to develop large-scale nutrition models to test bottom-up effects on population performance is challenging (Pastor 2011). Our landscape nutrition models focused on differences in the abundance, digestibility, and phenological stage of forage plant species as revealed by diet during late summer, a period recently highlighted to be perhaps the greatest driver of ungulate population responses (Cook et al. 2013). Landscape nutrition models represent an important breakthrough that allows ecologists to expand studies of foraging ecology to large enough scales to examine population performance based on bottom-up influences. Comparison of our approach to other previously published landscape nutrition models confirms similar predictive power (e.g., R^2 in previous studies cited below range from 0.1 to 0.6; Avgar et al. 2015) and insights that are gained in understanding the nutritional landscape for large herbivores. Early studies noted spatial variation in plant nutrition driven by rainfall, soil, and elevational gradients (Seagle and McNaughton 1992), but few explicitly linked such early models to ungulate performance. In one of the few models that linked landscape nutrition to ungulate performance, Albon and Langvatn (1992) modeled the effect of increasing elevation on crude protein available to migratory ungulates in Norway. These authors showed that with this single covariate, the nutritional benefits of elevational migration could be observed in higher fecal nitrogen, which resulted in higher body mass and survival (Mysterud et al. 2001). Building on Albon and Langvatn's approach, Hebblewhite et al. (2008) linked remotely sensed measures of vegetation productivity to plot-level nutritional resources to develop a spatiotemporally dynamic landscape nutrition model over a 5,000-km² area. This landscape nutrition model revealed that because of higher access to nutritional resources during the migratory season, winter calf weights and pregnancy rates of migratory elk were higher than those of non-migratory elk. Since then, others have developed similar large-scale landscape nutrition models for browsing moose (*A. alces*; van Beest et al. 2010), domestic sheep (Mysterud et al. 2011), elephants (*Loxodonta Africana*; Pretorius et al. 2011); and woodland caribou (*Rangifer tarandus caribou*; Avgar et al. 2015), and, importantly, used these models to test hypotheses about how bottom-up factors affect population dynamics. Other approaches toward understanding ungulate nutritional resources are also feasible, including evaluation of above-ground net production and utilization (Wisdom et al. 2006, Lehmkuhl et al. 2013) and use of tame animals to determine dietary composition and quality (Cook 2002). Additionally, the use of tame animals offers several advantages in establishing relationships between nutritional resources and population dynamics, as tame animals may be used in experiments designed to understand effects of variable

nutritional resources on animal reproduction and survival (Cook et al. 2004). Despite the inherent challenges of scaling-up from plot-level or animal-level to landscape-levels, we recommend development and evaluation of landscape nutrition models for large herbivores as a tool to understand consequences of environmental change, which will be especially important in an era of changing land use and large herbivore migratory behaviors (Berger 2004).

Ungulate migratory behavior has the potential to affect the landscape-nutrition-body-condition-pregnancy relationship (Hebblewhite et al. 2008). The use of distinct seasonal habitats by migratory ungulates allows access to seasonally high-quality forage and can reduce predation risk (Fryxell and Sinclair 1988). Populations exposed to similar nutritional resources on their summer ranges could have different levels of nutritional exposure and body fat if they spend different amounts of time on their summer ranges due to human activity, such as early-fall hunting, if a portion of the population does not migrate to summer ranges or if differences in phenology exist among summer ranges. In our study area, the West Fork elk spent considerably less time on their summer range than East Fork elk (West Fork mean = 53 d, East Fork mean = 138 d; *unpublished data*, this study) and a lower proportion of the population displayed traditional migratory behaviors (West Fork = 49%, East Fork = 78%; *unpublished data*, this study). However, the duration of summer range use was more likely a response to the differences in available nutritional resources than responses to human activities on the summer ranges. The West Fork population is exposed to very restrictive hunting regulations and experiences minimal hunting pressure, while the East Fork population is exposed to more liberal either sex hunting regulations and experiences considerably more hunting pressure. Therefore, while human activities such as hunting have the potential to affect how elk are utilizing their seasonal ranges, in this case it is unlikely that human activity would drive West Fork elk from their summer ranges and alter the landscape-nutrition-body-condition-pregnancy relationship. Additionally, phenological differences in the rate and duration of green-up may affect the landscape-nutrition-body-condition-pregnancy relationship for migratory elk (Middleton et al. 2013a); however, in our study we did not observe differences in forage plant phenology in the West Fork and East Fork summer range and differences in phenology did not appear to drive the observed differences in body condition and pregnancy rates between populations.

Understanding the relative effects of bottom-up and top-down factors on ungulate populations will be crucial to developing appropriate management strategies to maintain ungulate populations at desired levels. Wildlife managers should identify ungulate populations that are nutritionally limited and be aware that these populations may be more impacted by recovering carnivores and more sensitive to the effects of harvest than more

productive populations (Melis et al. 2009). Managers may consider applying conservative ungulate harvest prescriptions, together with liberal carnivore harvest prescriptions, in these areas. Habitat treatments that increase nutritional resources on summer ranges may benefit ungulate populations. In our study area, wildfire in both low-elevation, dry forests and higher-elevation, wet forests produced similar increases in nutritional resources on average. However, nutritional resources also varied with elevation and aspect, so the actual effects of wildfire may depend on fire location on the landscape. We expect that maintaining a mosaic of fire history and distribution will benefit ungulate species, as composition-induced changes in nutritional resources may initially decrease post fire, reach a peak 6–15 years post fire (e.g., Sachro et al. 2005), then decrease as the forest ages.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/eap.1370/supinfo>

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.2hb22.2>